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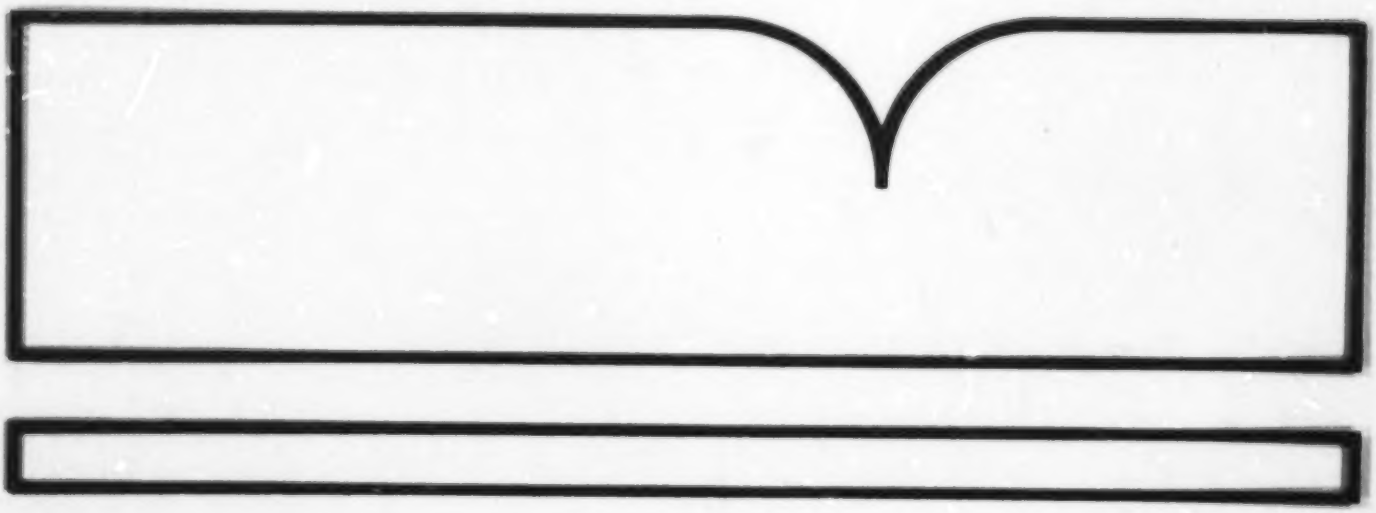

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16. ABSTRACT

Stomatal conductance and transpiration were measured on normally-irrigated (NI) and water-stressed (WS) field-grown cotton (Grossypium hirsutum L.) exposed throughout the growing season to a gradient of ozone (O_3) concentrations. Environmental conditions during the growing season strongly affected stomatal responses and yield reductions due to O_3 exposure. Maximum stomatal conductance and transpiration decreased with increased O_3 concentration both in NI and WS treatments. Maximum conductance in severely O_3-Stressed plants averaged 30% lower than charcoal-filtered (control) plants, but maximum transpiration was only 17% lower. Conductance in WS plots averaged 22% lower than in NI plots but transpiration rates were the same in both treatments. Yield reductions induced by O_3 were highly correlated (r^2=0.84) with daily transpiration. Stomata of O_3-stressed plants opened and closed at the same rate as control plants in response to changes in light intensity, suggesting that the mechanism of stomatal movement had not been impaired by exposure to O_3. Reductions in conductance and transpiration in O_3-stressed plants were attributed to inhibition of photosynthesis by O_3, leading to accumulation of CO_2 in intercellular spaces.

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Stomatal conductance and transpirational responses of field-grown cotton to ozone

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Abstract. Stomatal conductance and transpiration were measured on normally-irrigated (NI) and water-stressed (WS) field-grown cotton (*Gossypium hirsutum* L.) exposed throughout the growing season to a gradient of ozone (O_3) concentrations. Environmental conditions during the growing season strongly affected stomatal responses and yield reductions due to O_3 exposure. Maximum stomatal conductance and transpiration decreased with increased O_3 concentration both in NI and WS treatments. Maximum conductance in severely O_3-stressed plants averaged 30% lower than charcoal-filtered (control) plants, but maximum transpiration was only 17% lower. Conductance in WS plots averaged 22% lower than in NI plots but transpiration rates were the same in both treatments. Yield reductions induced by O_3 were highly correlated ($r^2 = 0.84$) with daily transpiration. Stomata of O_3-stressed plants opened and closed at the same rate as control plants in response to changes in light intensity, suggesting that the mechanism of stomatal movement had not been impaired by exposure to O_3. Reductions in conductance and transpiration in O_3-stressed plants were attributed to inhibition of photosynthesis by O_3, leading to accumulation of CO_2 in intercellular spaces.

Key-words: Gossypium hirsutum L.; Malvaceae; cotton; stomatal conductance; transpiration; ozone; drought stress.

Introduction

The capacity of plants to assimilate CO_2 is controlled by stomatal conductance and by internal biochemical and physiological factors that control the photosynthetic process. Recent evidence has suggested that both stomatal conductance (g) and photosynthetic capacity are coordinated in a manner that optimizes daily assimilation rates (A) and transpiration rates (E) such that the ratio $(\delta A/\delta g)/(\delta E/\delta g)$ remains relatively constant (Cowan & Farquhar, 1977; Wong, Cowan & Farquhar, 1979; Farquhar, Schulze & Küppers, 1980; Hall & Schulze, 1980; Farquhar & Sharkey, 1982). This relationship between assimilation of CO_2 and transpiration provides the physiological basis for models of crop yield as a function of seasonal transpiration (Hanks, 1974; Hanks & Hill, 1980). Stomata also play a major role in regulating plant responses to atmospheric pollutants (Mansfield, 1973; Unsworth & Black, 1981). Environmental factors conducive to open stomata and active gas exchange, such as high relative humidity and adequate soil moisture, increase pollutant uptake and subsequent development of foliar injury symptoms (Setterstrom & Zimmerman, 1939; Otto & Daines, 1969; Rich & Turner, 1972; Davids, Davis & Pennypacker, 1981; Tingey *et al.*, 1982).

Air pollutants themselves can affect stomatal movement. Resistant cultivars of onion (*Allium cepa* L.) and pinto bean (*Phaseolus vulgaris* L.) close stomata rapidly or more completely than susceptible cultivars in the presence of ozone (O_3) (Engle & Gableman, 1966; Knudson-Butler & Tibbitts, 1979). Hill & Littlefield (1969) reported simultaneous reductions in apparent photosynthesis and transpiration and stomatal closure in response to O_3 in a variety of plant species. Although stomatal opening in response to O_3 has been reported (Evans & Ting, 1974; Olszyk & Tibbitts, 1981), most evidence indicates that conductance and transpiration decrease in response to O_3 (Unsworth & Black, 1981).

Studies of conductance and transpirational responses to O_3 have, with few exceptions, been conducted on potted plants exposed under laboratory conditions for short periods of time. Relatively little is known of the effects of O_3 on stomatal responses of plants grown and exposed under field conditions. Coyne & Bingham (1978) found that O_3 at 0.072 $cm^3\ m^{-3}$* decreased stomatal conductance in field-grown *Phaseolus vulgaris* L. Seasonal trends of photosynthesis and stomatal conductance of O_3-injured *Pinus ponderosa* Laws. showed that the most severely injured trees had lower photosynthetic rates but higher maximum stomatal conductances on current and 2-year-old needles compared with trees showing little or no injury development. Conductance of 1-year-old needles showed the greatest seasonal decline in response to O_3 (Coyne & Bingham, 1981, 1982).

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*Note: 1 $cm^3\ m^{-3}$ of O_3 = 1997 $\mu g\ m^{-3}$ at NTP.

Plants exhibit progressively declining rates of conductance and transpiration in response to depletion of available soil moisture (Bates & Hall, 1982). Reduced stomatal conductance under drought conditions could protect plants from the effects of O_3 by reducing its flux to internal leaf surfaces. Thus, experimental protocols in which crops are exposed to O_3 under optimum soil moisture conditions may overstate O_3 responses in comparison with actual field conditions in which plants are subjected to periodic or occasional drought. The present study was conducted to determine responses of conductance and transpiration in irrigated and drought-stressed cotton (*Gossypium hirsutum* L.) exposed to O_3, and to relate these responses to yield reductions induced by the pollutant.

Materials and methods

This experiment was conducted at the USDA Cotton Research Station in Shafter, CA, in a rural agricultural area upwind of any local sources of industrial or urban air pollution. Cotton seed (cv. 'Acala SJ-2') was planted at 102 cm row-spacings on 21 April 1982. Thirty plots were marked off on 7.6 m centres and each was dyked to allow for individual furrow-irrigation. Plots were assigned at random to normal irrigation (NI) or water-stressed (WS) treatments. NI plants were irrigated when leaf xylem water potential (ψ_l) averaged -1.8 MPa; WS plants were watered at -2.0 MPa (Grimes & Yamada, 1982). Xylem water potentials were measured at solar noon by pressure bomb (Plant Water Status Console, Model 3000; Soil Moisture Equipment Corporation, Santa Barbara, CA). Total seasonal irrigation averaged 69.4 ± 2.8 cm to NI plots and 55.6 ± 2.3 cm to WS plots. Details of plot layout, cultivation practices, and irrigation treatments are given in Temple, Taylor & Benoit (1985).

On 2 June 1982, when plants were in the 2–3 true leaf stage, 24 cylindrical open-top chambers 3 m in diameter and 2.4 m high were centred on randomly-selected plots. Each chamber contained two centre sample rows and two guard rows. Two additional rows were located just outside chamber walls. The 24 chambers were assigned at random to six O_3 treatments, each replicated four times. O_3 levels were: (i) full charcoal filtration (CF); (ii) half-filtered (NF × 0.5); (iii) non-charcoal filtered (NF); (iv) NF plus 1/3 of ambient O_3 concentration (NF × 1.3); (v) NF plus 2/3 of ambient O_3 (NF × 1.7) (vi) double ambient O_3 (NF × 2.0). Ozone was added in direct proportion to its concentration in ambient air so that the diurnal pattern of O_3 concentrations in the chambers paralleled normal ambient O_3 fluctuations. Open plots (AA) were used as non-chamber controls. O_3 additions began on 2 June and continued 7 h d^{-1} (0900–1600) until 9 September. Chamber blowers operated 15 h d^{-1} (0600–2100). Ambient chamber, and open plot O_3 concentrations were monitored by Dasibi ozone analysers (Model 1003-AH: Dasibi Environmental Corp., Glendale, CA) calibrated twice weekly with a transfer standard calibrated by the California Air Resources Board. Sample air from each chamber or AA plot was collected 10 cm above canopy height through continuously-aspirated Teflon lines 46 m long. Each line was sampled for an average of 5 min h^{-1} (Temple *et al.*, 1985). Ambient O_3 was continuously monitored at a height of 3 m. Ambient SO_2 was monitored at the same height with a Monitor Labs SO_2 Analyzer (Model 8850, Monitor Labs., Inc., San Diego, CA).

Open bolls were harvested from 2 m sections of the two centre rows in chambers or AA plots on 20–21 October 1982. The bolls were ginned at 5.5% moisture. Pre-gin bulk weight and lint and seed weights were recorded for each sample. A similar experiment on cotton was conducted in 1981, except that WS plots received 64 mm of water when average ψ_l reached -2.1 MPa; NI plots received 76 mm of water when average ψ_l reached -1.8 MPa.

Stomatal conductance and transpiration measurements were taken at monthly intervals during the exposure period. Charcoal-filtered, NF, and NF × 2.0 chambers, and AA plots at both levels of soil moisture were sampled between 1030–1430 PST to establish maximum stomatal conductance for each treatment. Five plants were selected at random within each chamber or plot and conductance and transpiration were measured on abaxial surfaces of the highest fully-expanded uninjured leaves of each plant using a steady-state porometer (Model LI-1600, LI-COR Inc., Lincoln, NB). A boundary layer resistance (R_a) of 0.0015 s m^{-1} was used to calculate transpiration. The porometer also measured light intensity, relative humidity, leaf and chamber temperatures. On 2 September, measurements were made from 0630 to 1930 PST to determine the complete diurnal stomatal response of these treatments. All plots had been irrigated 6–8 d previously.

A shading experiment was conducted on 3 September to compare stomatal response of NI plants to changes in light intensity. At 0915, the south rows of one CF and NF × 2.0 chamber were shaded by double layers of 75% shade cloth, and measurements of stomatal conductance, transpiration, and light intensity were made at 15 min intervals on five plants in both shaded south rows and unshaded north rows. Measurements were made as previously described. Shading was removed after 2 h, and stomatal re-opening was monitored for an additional hour.

Results

Daily weather data obtained from meteorological stations at Shafter indicated that growing conditions in the Central Valley of California in 1982 were cooler and more humid than average, particularly in comparison with 1981. Monthly mean pan

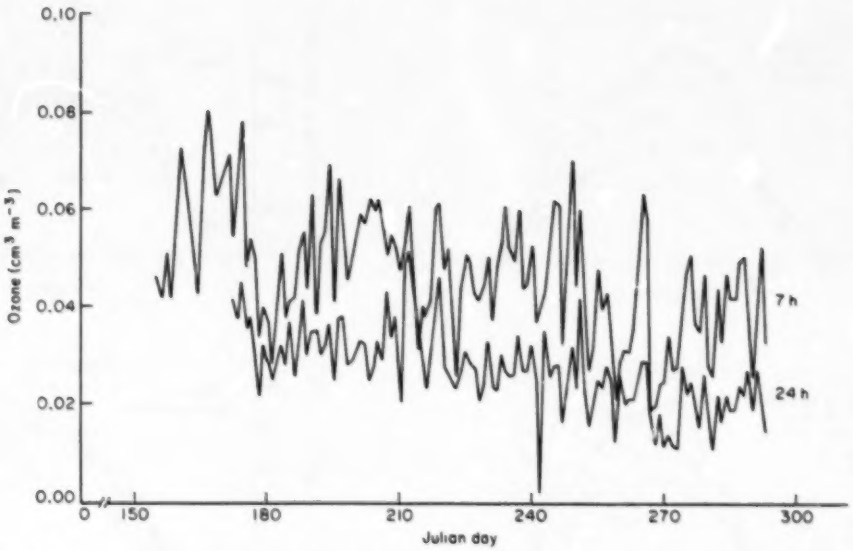

Figure 1. Daily 7 (0900–1600) and 24 h mean ambient ozone concentrations in Shafter, CA, during the 1982 growing season for cotton.

evaporation and accumulated degree d above 15.5 °C averaged 20% lower in June, July and August of 1982 than in 1981. Ambient O_3 averaged 36% lower in 1982 than in 1981. Seasonal 7 h (0900–1600 H PST) mean ambient O_3 concentration in 1982 was 0.047 cm^3 m^{-3}. In 1981 the seasonal 7 h mean ambient O_3 concentration was 0.077 cm^3 m^{-3}. Seasonal fluctuations in 7 h and 24 h mean O_3 concentrations are shown in Fig. 1. Ambient SO_2 concentrations were at or near 0 for the entire growing season.

Mean maximum abaxial stomatal conductance and transpiration for July–September are given in Table 1. Highest maximum conductances were found in normally irrigated (NI) open (AA) plots. Conductance in water-stressed (WS) AA plots averaged 21% lower than in non-stressed plots. Inside chambers WS plants tended to have lower maximum conductances than NI plants, but these differences were not statistically significant. Plants inside chambers showed reduced maximum conductance with increased exposure to O_3. Conductance of NI plants exposed to a seasonal 7 h mean O_3 concentration of 0.092 cm^3 m^{-3} (NF × 2.0) averaged 30% lower than that of plants grown in charcoal-filtered (CF) air (seasonal 7 h mean O_3 = 0.012 cm^3 m^{-3}). Plants in non-filtered (NF) chambers (seasonal 7 h mean O_3 = 0.044 cm^3 m^{-3}) averaged 15.5% lower maximum conductance than those in CF chambers. Ozone effects on conductance of water-stressed plants were not as pronounced, particularly at the highest O_3 concentration. Conductance was reduced 17% and 19% in NF and NF × 2.0 treatments, respectively, compared with that of CF plants.

Similar trends were seen in transpiration rates

Table 1. Mean maximum abaxial stomatal conductance and transpiration of normally-irrigated (NI) and water-stressed (WS) cotton exposed to ozone in open-top chambers.

Treatment*	$[O_3]$† (cm^3 m^{-3})	Conductance ($m\ s^{-1} \times 10^2$)		Transpiration ($\mu g\ m^{-2}\ s^{-1} - 10^{-4}$)	
		NI	WS	NI	WS
CF	0.012	0.90±0.14	0.78±0.14	12.69±3.83	11.19±3.93
NF	0.044	0.76±0.11	0.65±0.13	10.63±4.31	10.62±0.36
NF × 2.0	0.092	0.63±0.04	0.63±0.08	10.06±2.49	9.45±2.96
AA	0.047	1.06±0.10	0.84±0.14	15.45±2.11	13.01±3.89

Data were collected between 1030–1430 on 4 d between 24 June and 3 September 1982, from five plants per treatment, ±s.d.

*Treatments were charcoal-filtered air (CF), non-filtered air (NF), twice ambient O_3 concentrations (NF × 2.0), and non-chambered plots (AA). Ozone was added in proportion to its concentration in ambient air for 7 h daily from 2 June to 9 September 1982.

†Seasonal 7 h (0900–1600) mean O_3 concentrations for four replicate chambers or AA plots.

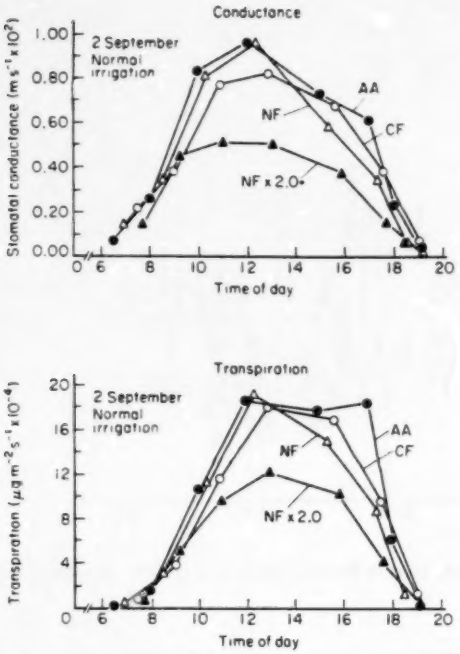

Figure 2. Diurnal course of abaxial stomatal conductance (a) and transpiration (b) for normally irrigated cotton exposed to charcoal-filtered air (CF); non-filtered air (NF); twice ambient ozone (NF × 2.0), and open (non-chamber) plots (AA); mean of five measurements per point.

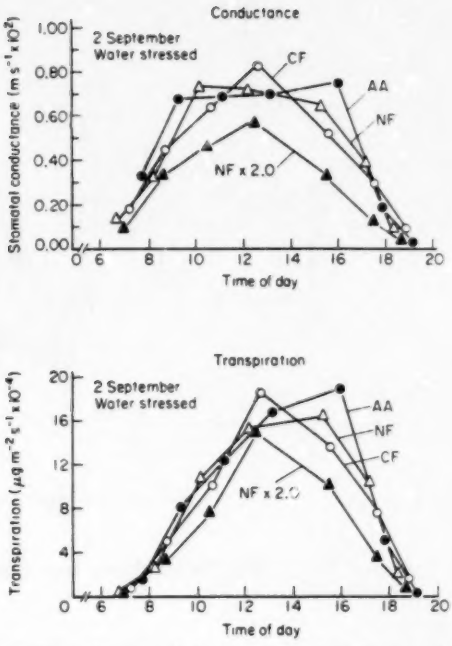

Figure 3. Diurnal course of abaxial stomatal conductance (a) and transpiration (b) for drought-stressed cotton. Abbreviations as in Fig. 1.

(Table 1). Highest rates of transpiration were found in NI AA plots, and WS plants averaged 16% lower maximum transpiration than NI plants. Inside chambers, CF plants had the highest rates and exposure to O_3 reduced transpiration in NI plots 16% and 21% in NF and NF × 2.0 treatments, respectively. Water-stressed plots showed less response to O_3, with transpiration rates reduced 5% and 16% in NF and NF × 2.0 treatments, respectively. Differences in transpiration rates between NI and WS plots were not statistically significant.

The diurnal course of stomatal conductance and transpiration for NI cotton on 2 September 1982 for four O_3 treatments are shown in Fig. 2a,b, respectively. Stomata in all treatments were fully open by 1000 and for all treatments stomata remained fully open until 1200–1400. Plants in NF × 2.0 treatments had significantly lower stomatal conductance than other O_3 exposures, averaging only 50% of maximum conductance of CF and NF treatments. Stomata in all treatments were fully closed by 1900. Stomatal conductance was most highly correlated with light intensity (data not shown). Transpiration rate peaked later in the day and remained higher later in the day than conductance (Fig. 2b). Rate of transpiration was most highly correlated with vapour pressure deficit (data not shown). Plants in NF × 2.0 chambers had significantly lower transpiration rates than other O_3 exposures, averaging 38% lower than the mean of CF and NF treatments. Diurnal curves of stomatal conductance and transpiration for WS plots were similar to those of NI plots (Fig. 3a,b). Stomata remained open and transpiration rates remained high until 1700–1800. Maximum conductance in WS plots averaged 22% lower than in NI plots, but rates of transpiration were the same in WS as in the NI plots. Plants in NF × 2.0 treatments had 30% lower maximum stomatal conductance than in CF or NF treatments, but transpiration was only 17% lower than other O_3 exposures.

Total daily transpiration for each O_3 treatment was computed by integrating the area under the curves of Figs 2b & 3b. Both water-stressed and non-stressed plots had about the same total transpiration, and plants in NF × 2.0 chambers had significantly lower daily transpiration than non-O_3 stressed plants. Total daily transpiration was highly correlated with lint yield ($\alpha < 0.01$; $r^2 = 0.84$) (Fig. 4). Cotton yield was also significantly reduced by increased O_3 concentrations. Lint yields were reduced 14% and 65% in NF and NF × 2.0 chambers, respectively, compared with CF controls. Yield reductions due to O_3 in WS plots were not significantly different from those in NI plots (Temple *et al.*, 1985).

Results of the shading experiment are shown in Fig. 5. Conductance in both CF and NF × 2.0 plants declined rapidly after 90% shade was applied. Conductance of shaded O_3-stressed plants was

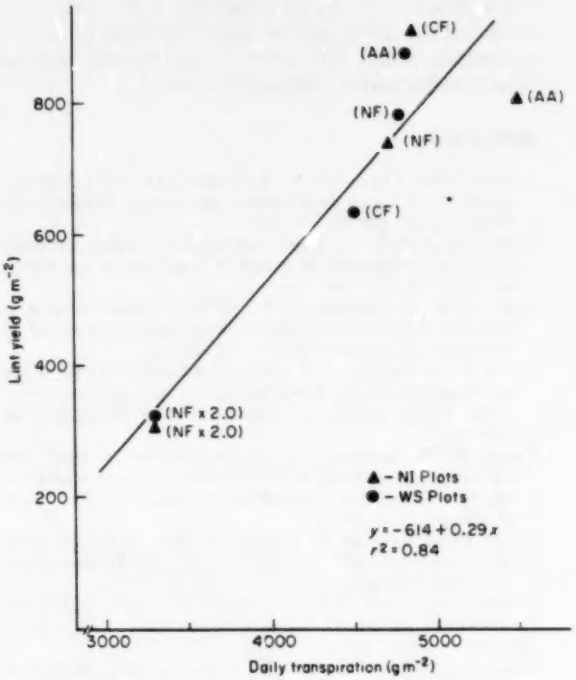

Figure 4. Lint yield and total daily transpiration of normally-irrigated (NI) and drought-stressed (WS) cotton as a function of O_3 exposure. Abbreviations as in Fig. 1.

significantly lower than that of shaded plants grown in CF air. Stomatal conductance in both CF and NF x 2.0 plants increased rapidly to levels of non-shaded plants 30 min after shading was removed. The rate of increase in conductance after removal of shading was the same in both O_3-stressed and non-stressed plants, indicating that the mechanism of stomatal movement had not been impaired in O_3-stressed plants.

Discussion

The degree of protection from O_3 afforded to plants by drought stress is a function of severity and timing of the stress in relation both to O_3 episodes and to critical or susceptible life stages of the plant. Plants exposed to O_3 during periods of low available soil moisture and high evaporative demand may avoid O_3 injury (Walker & Vickery, 1961; Macdowall, Mukammal & Cole, 1964; Dean & Davis, 1967). Injury avoidance is associated with reduced stomatal conductance (Adedipe, Khatamian & Ormrod, 1973; Tingey *et al.*, 1982). In 1981, during typical summer growing conditions in the San Joaquin Valley, when mean daily pan evaporation exceeded 10 mm d^{-1}, ψ_l of WS plants frequently exceeded −2.1 MPa 8–10 d past irrigation. Plants wilted in late morning or early afternoon. Stomata close and assimilation of CO_2 ceases in cotton under these conditions (Grimes & Yamada, 1982). These plants had significantly lower yields than NI plants and showed no response to O_3 except at the very highest O_3 concentrations used in the experiment (Temple *et al.*, 1985). In contrast, mean daily pan evaporation during the summer of 1982 rarely exceeded 8 mm d^{-1} and ψ_l of WS plants rarely exceeded −2.0 MPa. Under these conditions, differences between normally irrigated and water-stressed plants were not as extreme as in 1981, and both had similar yield responses to O_3 (Temple *et al.*, 1985).

Chronic exposure to O_3 reduced stomatal conductance and transpiration in this study and the amount of reduction increased with increased exposure to

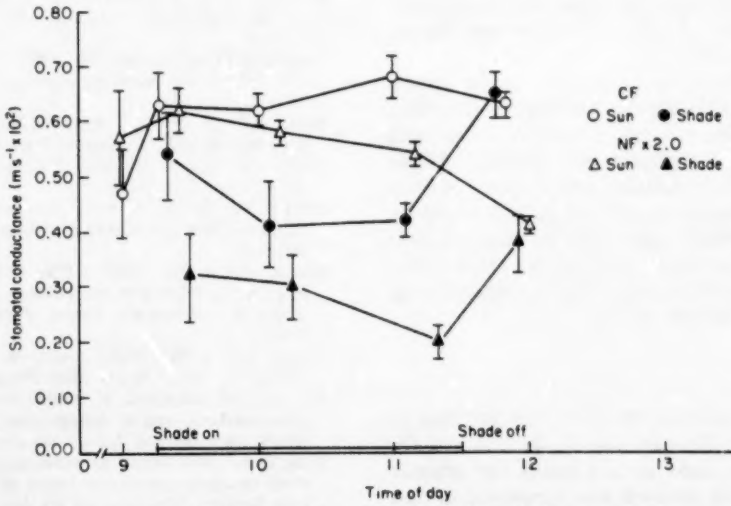

Figure 5. Stomatal responses of O_3-stressed (NF x 2.0) and non- stressed (CF) cotton to rapid changes in light intensity. Each point is a mean of five measurements ±s.d.

O_3. Conductance was more sensitive than transpiration to inhibition by O_3. Coyne & Bingham (1978) also found greater relative reduction in rates of maximum conductance than net photosynthesis in field-grown *Phaseolus vulgaris* L. exposed to O_3. The mechanism of O_3-induced stomatal closure has not been satisfactorily explained. The suggestion that O_3 inhibits photosynthesis leading to accumulation of CO_2 in intercellular spaces, with subsequent stomatal closure, is not fully supported by experimental evidence. Hill & Littlefield (1969) reported that stomatal closure occurred before, or simultaneous with, decreases in net photosynthesis. Stomatal closure due to pollutant exposure also occurs several times more rapidly than exposure to elevated CO_2 (Heath, 1980). Heath (1980) suggested that O_3 (or secondary toxic metabolites) travelled with apoplastic water flow to the stomatal epidermal region where it can alter membrane permeability, leading to increased epidermal transpiration or altered guard cell-subsidiary cell turgor pressure relationships, thus inducing stomatal closure. In the shading experiment, stomata of O_3-stressed plants closed rapidly in response to reduced light and opened at the same rate as non-O_3-stressed plants in response to increased light intensities, indicating that the stomatal mechanism itself was not affected by O_3 stress. Stomata of severely O_3-stressed plants also showed normal diurnal responses, including full stomatal closure at sunset. The only differences in stomatal response between plants exposed to twice ambient O_3 concentrations and non-O_3 stressed plants were a 30–50% reduction in maximum daily conductance and 25% lower conductance in response to low light levels in the shading experiment. These results are consistent with a model of stomatal closure based on O_3-induced impairment of photosynthetic capacity, leading to increased internal CO_2, with subsequent stomatal closure. Reduced photosynthetic capacity in response to chronic exposure to O_3 has been reported in several plant species (Reich, 1983; Reich *et al.*, 1986).

The high correlation between daily transpiration and cotton yield ($r^2 = 0.84$) observed in this field experiment is consistent with models of crop yield based on seasonal transpiration (Hanks, 1974). These results are also consistent with a model of crop yield based on seasonal water use as influenced by O_3 stress (King, 1984). These results indicate that measurements of stomatal conductance and transpiration may be useful in predicting O_3-induced crop yield losses in field-grown cotton.

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